

Seasonal changes of soil respiration in *Betula platyphylla* forest in Changbai Mountain, China

LIU Ying^{1,2}, HAN Shi-jie², LIN Lu¹

¹ State Key Laboratory of Pulp and Paper Engineering, College of Light Industry and Food Sciences, South China University of Technology, Guangzhou 510640, P. R. China

² Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, P. R. China

Abstract: A study was conducted to determine the seasonal changes of soil respiration and the contribution of root respiration to soil respiration in *Betula platyphylla* forest in Changbai Mountain from May to September in 2004. Results indicated that the total soil respiration, root-severed soil respiration and the root respiration followed a similar seasonal trend, with a high rate in summer due to wet and high temperature and a low rate in spring and autumn due to lower temperature. The mean rates of total soil respiration, root-severed soil respiration and root respiration were 4.44, 2.30 and 2.14 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively during the growing season, and they were all exponentially correlated with temperature. Soil respiration rate had a linear correlation with soil volumetric moisture. The Q_{10} values for total soil respiration, root-severed soil respiration and root respiration were 2.82, 2.59 and 3.16, respectively. The contribution rate of root respiration to the total soil respiration was between 29.3% and 58.7% during the growing season, indicating that root is a major component of soil respiration. The annual mean rates of total soil respiration, root-severed soil respiration and root respiration were 1.96, 1.08, and 0.87 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, or 741.73, 408.71, and 329.24 $\text{g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$, respectively. Root respiration contributed 44.4% to the annual total soil respiration. The relationship proposed for soil respiration with soil temperature was useful for understanding and predicting potential changes in Changbai Mountain *B. platyphylla* forest ecosystem in response to forest management and climate change.

Keywords: root respiration; seasonal variations; soil respiration; soil temperature; soil water content

Introduction

As the research on global climate change becomes one of the focuses of the public and scientific group, the measurements of source or sink of CO_2 have been noticed. Soil, as a huge carbon pool (1.394×10^{18} g C) (Raich & Schlesinger 1992), is an important source or sink of atmospheric CO_2 . Manipulation of soils to increase their carbon storage capacity has been proposed as a method for slowing the rate of atmospheric CO_2 increase (IPCC 1996). The carbon balance of terrestrial ecosystems plays a major role in regulation of the surface temperature of the earth (Schimel 1995). The regulation of net primary production has

been well known for most of the earth's ecosystem; however, our knowledge about belowground respiration processes is quite poor (Raich & Potter 1995).

Soil CO_2 efflux is the result of autotrophic respiration by roots and associated mycorrhizae, and heterotrophic respiration by microorganisms and soil fauna that decompose aboveground litter and belowground detritus and soil organic matter. Despite the growing body of information on soil respiration processes, partitioning between autotrophic and heterotrophic respiration remains clearly unresolved and the issue of how different components of soil respiration are likely to respond to climate change is highly controversial (e.g. Kirschbaum 1995; Trumbore et al. 1996; Giardina & Ryan 2000).

As a result of climate change, and the increasingly recognized importance of the role of soils now and in the future, more efforts are being put into making better estimates of soil CO_2 efflux and its components to improve our understanding of the interactions between environmental variables and soil respiration. It is difficult to partition the soil CO_2 efflux between autotrophic and heterotrophic respiration. Hanson et al. (2000) reviewed the different methods and approaches for separating root and soil microbial contributions to soil respiration. Early attempts were made by removing roots from the soil in the laboratory (e.g. Wiandt 1967), or by measuring the respiration of roots *in situ* directly after removing the soil around them (e.g. Edwards & Sollins 1973). Estimates have also been made by finding the relationship

Foundation project: This study was supported by the Knowledge Innovation Project of the Chinese Academy of Sciences (KZCX2-YW-416) and the National Natural Science Foundation (90411020).

Received: 2009-03-26; Accepted: 2009-06-22

© Northeast Forestry University and Springer-Verlag 2009

The online version is available at <http://www.springerlink.com>

Biography: Liu Ying (1976-), female, Ph. D., Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, P. R. China.

E-mail: liuyingamy@163.com

Corresponding author: Prof. HAN Shi-jie, E-mail: liuyingamy@163.com

Responsible editor: Hu Yanbo

between soil respiration and fine root biomass using simple regression analysis (Kucera & Kirkham 1971; Xu & Qi 2001). Other attempts were also made to dig trenches around small areas to exclude roots, and hence to eliminate root growth and respiration (e.g. Bowden et al. 1993; Boone et al. 1998; Epron et al. 1999). More recently isotopic approaches have been developed. The isotopic signal of the soil CO₂ efflux was used to derive the partitioning (Hanson et al. 2000). Although such methods have obvious advantages because of the lack of soil and root disturbance, the high costs and complexity of the analyses limited their use to a few situations in boreal forest (Thrumore et al. 1996; Ekblad & Högberg 2001) and elevated CO₂ studies (Lin et al. 1999). Very recently, a novel estimation of the root contribution to total soil respiration of Scots pine has been made in a large-scale girdling experiment, in which the phloem was cut away on 720 trees, in a fully replicated design, while the xylem continued to allow water movement (Högberg et al. 2001). These different methods all have intrinsic limitations associated with either the sampling methodology or changes in soil conditions as a consequence of the absence of living roots and increased input of root detritus to the soil, and have yielded estimates of root respiration ranging from 10% to 90% of the total (Hanson et al. 2000).

In the present study, we used subtraction method (Gansert 1994; Högberg et al. 2001) and LI-6400-09 soil respiration chamber (LI-COR Inc., Lincoln, Nebraska, USA) to measure *in situ* soil respiration rates with and without root-severed. Based upon the field data on seasonal variation of soil respiration, we could obtain the response of soil respiration to the temperature and moisture and the contribution of root respiration to total soil respiration. The objectives of this study were to evaluate (1) the seasonal variation of soil respiration and its components in *Betula platyphylla* forest, (2) the relative importance of soil temperature and soil moisture as predictors of soil respiration, (3) the relative contribution of root respiration to the total soil CO₂ efflux, and (4) the annual soil CO₂ efflux.

Materials and methods

Site description

The study site was located on the north slope of Changbai Mountains, Jilin Province, northeast China (latitude 42°24'N and longitude 128°28'E, 738 m in elevation). The local climate is classified as cool-temperate. Annual mean temperature is 4°C and the annual mean precipitation is 700 mm. The site is covered with snow from October to the next April. Trees produce leaf buds at the beginning of May, and leaves begin to senesce in the end of September.

A 50-year-old secondary *B. platyphylla* forest was chosen at the site, with mean canopy height of 26 m and a dense understory consisting of decades of kinds of broad-leaved shrub and Korean pine (*Pinus koraiensis*) seedlings. The mean height of understory is 0.5–2 m. The soil is classified as dark brown forest soil originating from volcanic ashes. The landscape is very flat.

Root severing

On May 5, 2003, we inserted steel cylinder with 10-cm inner diameter into 30-cm depth of soil (approximately the bottom of the root zone) to sever all roots. The roots were not removed. We replaced the steel cylinder by PVC (polyvinyl chloride) cylinder whose inner diameter was the same to steel cylinder. Five replicates were made in the site.

To kill the roots in the cylinders, the aboveground parts of all plants growing in the plots were cut off at the soil surface. New seedlings and regrowth from the roots were periodically clipped when necessary.

Measurement of soil respiration

Soil collars made of PVC, 10 cm in diameter and 4.5 cm long, were inserted 2.5 cm into the soil next to each PVC cylinder. Once inserted, the collars were left in place throughout the course of the experiment. Soil respirations both inside the cylinders and soil collars were measured about once a week from May to September in 2004. The soil respiration chamber was coupled to a LI-6400 photosynthesis system that computes the emissions coming from the soil to the chamber. Following each measurement mode, we calculated the flux using the best fit of a linear regression, which computes several CO₂ flux measurements from the soil to the chamber. The system operation avoids over pressures of CO₂ inside the chamber by operating between a maximum and minimum CO₂ concentrations. The rate of increase in CO₂ concentration inside the chamber was monitored and the soil CO₂ emission was computed when the chamber CO₂ concentration is equal to that at the soil surface in the open. Thus, the contribution of roots to total soil respiration could be obtained by the difference between the values inside the cylinders and soil collars.

Measurement of temperature and moisture

Soil temperatures at 5 cm depth were recorded by Hobo thermal recorder (at 1-h interval). Soil water content was measured by TDR.

Estimation of year-round soil respiration and the contribution of root

We selected the Q₁₀ relationship to analyze the temperature dependence of soil respiration. The exponential function, $R = R_0 e^{bt}$, was used to describe the temperature dependence of soil respiration. Where R is the soil respiration (μmol·m⁻²·s⁻¹), R_0 the respiration rate at a reference temperature of 0°C, b is the coefficient related to Q₁₀ (sensitivity to temperature), i.e. Q₁₀ is the factor by which a reaction increases for an increase of 10°C ($Q_{10} = e^{10b}$), and t is the soil temperature (°C) at 5 cm depth.

Year-round soil respiration and the contribution of root were calculated on the basis of the Q₁₀ relationship and the average of daily soil temperatures at 5 cm depth.

Results

Seasonal changes in temperature and soil respiration

Air temperature varied more markedly than the soil temperature at 5 cm depth during the growing season in 2004. Total soil respiration and root-severed soil respiration varied with the changes in soil temperature at 5 cm depth (Fig. 1), and they increased steadily during spring following the increases in temperature until July when they reached the peak of $6.65 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and $3.47 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively.

As expected, total soil respiration and root-severed soil respiration became lower when soil temperature was lower. The seasonal change for total soil respiration and root-severed soil respiration was almost the same (Fig. 1). The total soil respiration rates ranged from $2.22 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to $6.65 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, which were higher than the root-severed soil respiration rates measured at the same time.

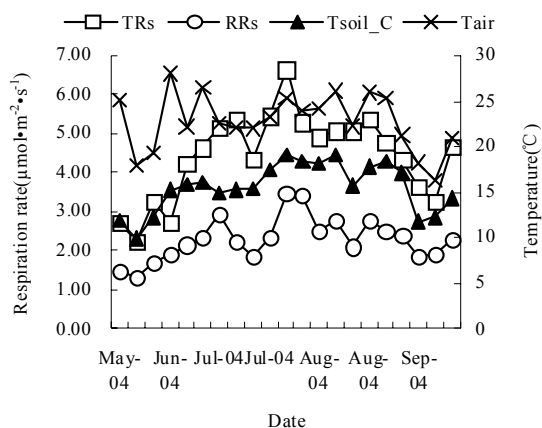


Fig. 1 Seasonal changes in soil respiration and temperature. TRs, RRs, T_{soil_C} , and T_{air} represent the total soil respiration, root-severed soil respiration, soil temperature at 5 cm depth, and air temperature 10 cm above ground, respectively.

Seasonal changes of root respiration and its contribution to the total soil respiration

The root respiration and its contribution to the total soil respiration were calculated by subtracting soil respiration rates measured in PVC cylinders from the rates measured in soil collars. It was observed that root respiration varied significantly with the change of season. It was lower at the beginning of growing season and increased with the increase of soil temperature (Fig. 2). During the growing season in 2004, the contribution of root respiration to the total soil respiration ranged from 29.3% to 58.7%.

Effects of soil temperature and soil moisture on the soil respiration

Total soil respiration, root-severed soil respiration and root respiration were exponentially related to soil temperature at the

depth of 5 cm (Fig. 3). Based on the correlations between soil respiration and soil temperature, we could figure out the Q_{10} values for total soil respiration, root-severed soil respiration and root respiration, which were 2.82, 2.59 and 3.16, respectively. There were linear correlations between soil respiration and soil volumetric moisture (Fig. 4).

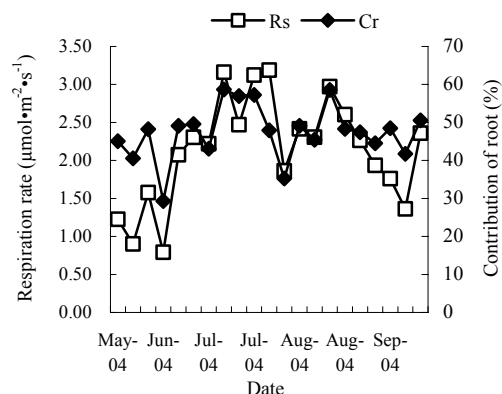


Fig. 2 Seasonal changes of root respiration and the contribution of root respiration to total soil respiration. Rs and Cr represent root respiration and the contribution of root respiration to total soil respiration, respectively.

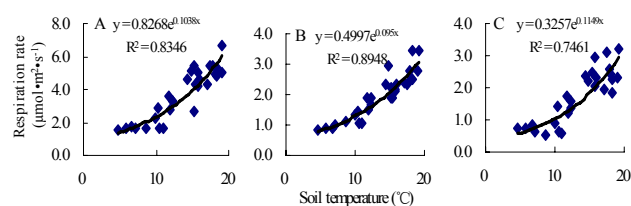


Fig. 3 The response of total soil respiration (A), root-severed soil respiration (B) and root respiration (C) to soil temperature at 5 cm depth.

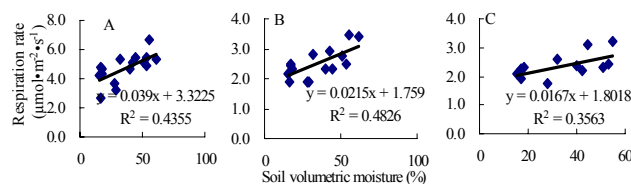


Fig. 4 The response of total soil respiration (A), root-severed soil respiration (B) and root respiration (C) to soil volumetric moisture above 10 cm depth.

Year-round soil respiration and the contribution of root respiration

Year-round total soil respiration and root-severed soil respiration (Fig. 5) estimated by Q_{10} relationship varied with the changes of soil temperature at 5 cm depth, increased with the increase of soil temperature from May to August in 2003, and decreased steadily with the decrease of soil temperature until the next May in 2004. The total soil respiration ranged from $0.76 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to $5.56 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and root-severed soil respiration ranged from $0.46 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to $2.86 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$.

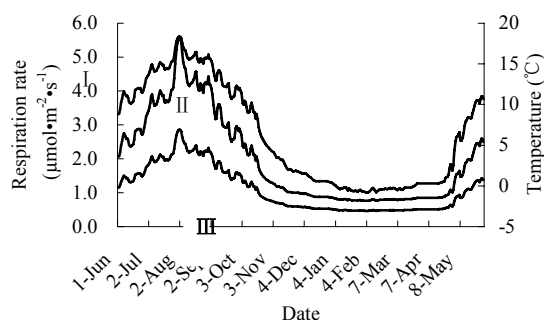


Fig. 5 Seasonal changes of soil respiration and temperature. I, II and III are soil temperature at 5 cm depth, total soil respiration and root-severed soil respiration, respectively.

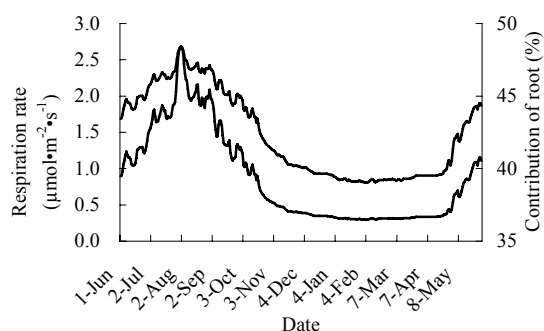


Fig. 6 Seasonal changes of root respiration and the contribution of root respiration to total soil respiration. I and II are the root respiration and the contribution of root respiration to total soil respiration, respectively.

The year-round variation of root respiration was almost the same with that of total soil respiration and root-severed soil respiration (Fig. 6). The maximum and the minimum of root respiration were $2.69 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and $0.30 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively. The year-round contribution of root respiration to the total soil respiration ranged from 39.0% to 48.3%.

The year-round mean of total soil respiration, root-severed soil respiration and root respiration were 1.96, 1.08, and $0.87 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, or 741.73, 408.71, and $329.24 \text{ g}\cdot\text{m}^{-2}\cdot\text{a}^{-1}$, respectively. Root respiration contributed 44.4% to the annual total soil respiration.

Discussion

The basic assumption of the root-severed method is that respiratory activity of roots severed is completely suppressed because of the lack of an energy supply. However, several studies have shown that the root excised from the main stem can survive and maintain respiration for some time after excision (Tate et al. 1993; Uchida et al. 1998). Moreover, in many cases, significant increases in root (or soil) respiration rates were observed immediately after root excision (or trenching), which can be attributed to injury by excision and disturbance to soil (Ewel et al. 1987; Uchida et al. 1998). In this study, high soil respiration rates after root severed were not observed; root-severed soil respiration rates in PVC cylinders were always lower than those of the soil

respiration in soil collars, indicating that root excision reduced root respiratory activity.

New root growth into the PVC cylinders from below the base was not prevented mechanically. However, most of the root was in the upper 30 cm of the soil, the effect of the root growth in the deep soil layer was regarded to be small.

The range of soil respiration rates measured in this study is similar to the range measured in other studies (e.g. Davidson et al. 1998; Law et al. 1999; Xu & Qi 2001; Rey et al. 2002). Similar diurnal and seasonal trends in soil respiration have also been observed elsewhere (e.g. Conant et al. 2000; Xu & Qi 2001; Lee et al. 2003).

There is large variability in the literature with regard to the relative contributions of autotrophic and heterotrophic respiration to total soil CO_2 efflux (as reviewed by Hanson et al. 2000). Estimates of root respiration, for example, range from 22% (Tate et al. 1993) to as much as 90% (Thierron & Laudelout 1996). As discussed earlier some of this large variability may be the result of differences in methodology, because it is difficult to measure the activity of roots without disturbing the soil, and partly the result of differences in forest and soil types (Hanson et al. 2000).

This study showed that the contribution of root respiration to the total soil respiration from May to September ranged from 29.3% to 58.7% and the annual mean contribution was 44.4%, which lay in the range of most forest in the world (30%–60%) (Singh et al. 2003). Ewel et al. (1987) and Epron et al. (1999) found a 60% contribution of root respiration in a 29-year-old slash pine plantation in Florida and in a 30-year-old beech forest in northern France, respectively. In a unique girdling experiment, Höglberg et al. (2001) found that 54% of the carbon assimilated by Scots pine in the Swedish boreal zone was respired by roots. By comparing soil respiration rates in a forest stand and in an adjacent stand where the roots were killed with a herbicide, Nakane et al. (1996) estimated that root respiration contributed 50% of total soil respiration. Together with other studies indicating similar figures, they suggested that the proportion of total soil respiration respired by roots may be fairly constant in forests that are close to equilibrium. Lee et al. (2003) found that root respiration is negligible by three months after root excision. Therefore, we could consider that the result of the contribution of root was reasonable.

Our Q_{10} for total soil respiration and root-severed soil respiration is in agreement with the median Q_{10} value for soil respiration in forest soils of 2.8 and 3.1, respectively, although the variance around this value is large (Raich & Schlesinger 1992; Kirschbaum 1995). Other studies have reported higher Q_{10} values for soil respiration. For example, Davidson et al. (1998) found Q_{10} values of 3.4 and 5.6, much higher than the values found in our study. They attributed this high value to the important contribution of roots to soil respiration. Pretzinger et al. (2000) reported a range of Q_{10} for root respiration of between 1.5 and 3. Lower values have been reported in other studies, such as the value of 1.8 found by Xu & Oi (2001) in a ponderosa pine forest in Northern California.

Respiration of both microbial communities and plant roots is sensitive to changes in soil temperature. We detected significant

differences in the sensitivity of the different respiring communities involved in total soil respiration. The root respiration had significant, slightly higher Q_{10} than total soil respiration and root-severed soil respiration. This was consistent with previous studies that have found a higher Q_{10} for root respiration, than for heterotrophic respiration (Boone et al. 1998; Epron et al. 1999). When a Q_{10} is calculated from a sequence of measurements taken over a period of time during which the temperature is changing, the resulting value may well be the product of the response of the respiratory process itself to temperature and the response of the population of respiring organisms, whether fine roots or micro-organisms, to temperature.

Linear correlation between soil respiration and soil moisture was found in this study. Soil moisture may affect soil respiration in two ways, either by limiting aeration, and thus the diffusivity of air, when it is high or by stressing soil microbial communities and root respiration when it is low.

Estimated annual soil respiration values (741.73 g m^{-2}) based on Q_{10} functions were well within the range of temperate *Quercus*-mixed forests ($610\text{--}1414 \text{ g m}^{-2}$) between 34°N and 45°N (Raich and Schlesinger 1992). Curtis et al. (2002) reported similar values for five eastern North American deciduous forests ($800\text{--}1\,207 \text{ g m}^{-2}$) between 36°N and 45°N .

As a complex ecological process, soil respiration is affected by many factors together. Further studies need to be carried out to analyze the influences of other ecological factors on soil respiration and to understand well the function of soil respiration and roots respiration in the global change.

Acknowledgements

This study was supported by the Knowledge Innovation Project of the Chinese Academy of Sciences (KZCX2-YW-416) and the National Natural Science Foundation (90411020). We are grateful to the staff of Changbai Mountain Forest Ecosystem Research Station for their help in the field work.

References

- Boone RD, Nadelhoffer KJ, Canary JD, Kaye JP. 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. *Nature*, **396**: 570–572.
- Bowden RD, Nadelhoffer KJ, Boone RD, Canary JD. 1993. Contributions of aboveground litter, belowground litter, and root respiration to total soil respiration in a temperate mixed hardwood forest. *Can J Forest Res*, **23**: 1402–1407.
- Conant RT, Klopatek JM, Klopatek CC. 2000. Environmental factors controlling soil respiration in three semiarid ecosystems. *Soil Sci Soc Am J*, **64**: 383–390.
- Curtis PS, Hanson PJ, Bolstad P, Barford C, Randolph JC, Schmid HP, Wilson KB. 2002. Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. *Agric Forest Meteorol*, **113**: 3–19.
- Davidson EA, Beld E, Boone RD. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biol*, **4**: 217–227.
- Edwards NT, Sollins P. 1973. Continuous measurement of carbon dioxide evolution from partitioned forest floor components. *Ecology*, **54**: 406–412.
- Eklblad A, Höglberg P. 2001. Natural abundance of ^{13}C in CO_2 respired from forest soils reveals speed of link between tree photosynthesis and root respiration. *Oecologia*, **127**: 305–308.
- Epron D, Farque L, Lucot E. 1999. Soil CO_2 efflux in a beech forest: the contribution of root respiration. *Ann For Sci*, **56**: 289–295.
- Ewel KC, Cropper WP, Gholz HL. 1987. Soil CO_2 evolution in Florida slash pine plantations. II. Importance of root respiration. *Can J Forest Res*, **17**: 330–333.
- Gansert D. 1994. Root respiration and its importance for the carbon balance of beech saplings (*Fagus sylvatica* L.) in a montane beech forest. *Plant Soil*, **167**: 109–119.
- Giardina CP, Ryan MG. 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature*, **404**: 858–861.
- Hanson PJ, Edwards NT, Garten CT, Andrews JA. 2000. Separating root and soil microbial contributions to soil respiration: A review of methods and observations. *Biogeochemistry*, **48**: 115–146.
- Höglberg P, Nordgren A, Buchmann N. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature*, **411**: 789–792.
- IPCC. 1996. Climate Change 1995. Impacts, Adaptations and Mitigation of Climate Change. Scientific-Technical Analyses, Cambridge University press, Cambridge, UK.
- Kirschbaum MUF. 1995. The temperature-dependence of soil organic-matter decomposition, and the effect of global warming on soil organic-C storage. *Soil Biol Biochem*, **27**: 753–760.
- Kucera CL, Kirkham. 1971. Soil respiration studies in tall grass prairie in Missouri. *Ecology*, **52**: 912–915.
- Law BE, Baldocchi DD, Anthoni PM. 1999. Below-canopy and soil CO_2 fluxes in a ponderosa pine forest. *Agr Forest Meteorol*, **110**: 27–43.
- Lee M, Nakane K, Nakatsubo T, Koizumi H. 2003. Seasonal changes in the contribution of root respiration to total soil respiration in a cool-temperate deciduous forest. *Plant Soil*, **255**: 311–318.
- Lin G, Ehleringer JR, Rygielwicz PT, Johnson MG, Tingey DT. 1999. Elevated CO_2 and temperature impacts on different components of soil CO_2 efflux in Douglas-fir terracosms. *Global Change Biol*, **5**(2): 157–166.
- Nakane K, Kohno T, Horikoshi T. 1996. Root respiration rate before and just after clear-felling in a mature, deciduous, broad-leaved forest. *Ecol Res*, **11**: 111–119.
- Raich JW, Schlesinger WH. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus*, **44B**: 81–89.
- Raich JW, Potter CS. 1995. Global patterns of carbon dioxide emissions from soils. *Global Biogeochem Cy*, **9**: 23–36.
- Rey A, Pegoraro E, Tedeschi V, Deparri I, Jarvis PG, Valentini R. 2002. Annual variation in soil respiration and its components in a coppice oak forest in Central Italy. *Global Change Biol*, **8**: 851–866.
- Schimel DS. 1995. Terrestrial ecosystems and carbon cycle. *Global Change Biol*, **1**: 77–91.
- Singh B, Nordgren A, Ottosson Lofvenius M, Höglberg MN, Emelland Ber PE, Höglberg P. 2003. Tree root and soil respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year. *Plant Cell Environ*, **26**: 1287–1296.
- Tate KR, Ross DJ, O'Brien BJ, Kelliher FM. 1993. Carbon storage and turnover, and respiratory activity, in the litter and soil of an old-growth southern beech (*Nothofagus*) forest. *Soil Biol Biochem*, **25**: 1601–1612.
- Thierron V, Laudelout H. 1996. Contribution of root respiration to total CO_2 efflux from the soil of a deciduous forest. *Can J Forest Res*, **26**(7): 1142–1148.
- Trumbore SE, Chadwick O A, Amundson R. 1996. Rapid exchange between soil carbon and atmospheric carbon dioxide driven by temperature change. *Science*, **272**: 393–396.
- Uchida M, Nakatsubo T, Horikoshi T, Nakane K. 1998. Contribution of micro-organisms to the carbon dynamics in black spruce (*Picea mariana*) forest soil in Canada. *Ecol Res*, **13**: 17–26.
- Wiant HV. 1967. Contribution of roots to forest soil respiration. *Adv Front Pl Sci*, **18**: 163–167.
- Xu M, Qi Y. 2001. Soil-surface CO_2 efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California. *Global Change Biol*, **7**: 667–677.